THE LARVA AND RELATIONSHIPS OF *CONONOTUS* LECONTE (COLEOPTERA: HETEROMERA)

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ABSTRACT

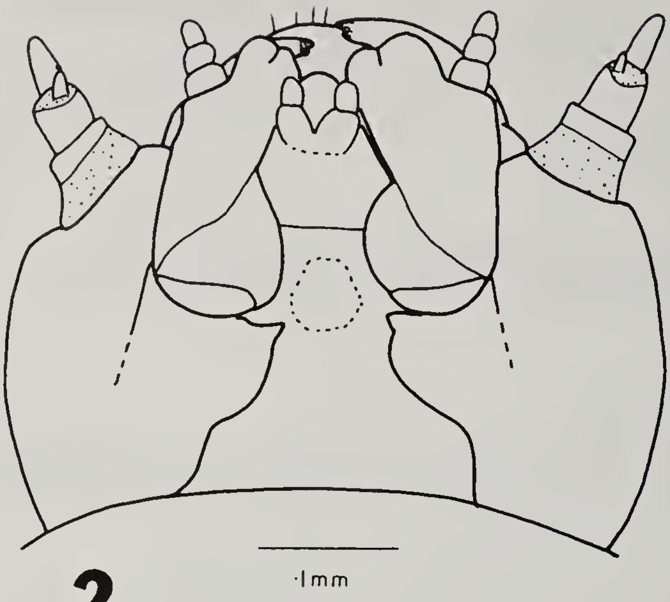
The larva of *Cononotus bryanti* Van Dyke is described and compared with larvae from related families of Heteromera. Larval characteristics suggest a very close relationship to the Palearctic genus *Agnathus* and to *Pedilidae (Pedilus,* but not *Pergetus*). It is proposed that Pedilidae should be considered a separate family from Anthicidae, based on larval characteristics. *Cononotus* and *Agnathus* would constitute the subfamily Cononotinae of Pedilidae.

The genus *Cononotus* LeConte includes 6 species of small beetles which superficially resemble anthicids. Based on the characteristics of the adults, *Cononotus* has been placed in the Pythidae or Salpingidae (LeConte and Horn 1883; Hatch 1965; Arnett 1968), the Lagriidae (Kaszab 1969), and in the Anthicidae (Abdullah 1974). Crowson (1953; 1967) recognized the close relationship of *Cononotus* to *Agnathus* Germar, and defined the new family Cononotidae based on these genera. When Crowson proposed Cononotidae the larva of *Cononotus* was unknown, and that of *Agnathus* very inadequately described. In addition, only the larva of *Pergetus* (=*Eurygenius*) *campanulatus* LeConte was described in the Pedilidae, and only the larvae of *Anthicus*, *Mecynotarsus*, and *Notoxus* among the Anthicidae. More recently the larvae of *Pedilus* (Mamaev 1976; Wharton 1979), *Agnathus* (Mamaev 1976), and of 6 additional genera of anthicids (Kitayama 1977) have been characterized. The purposes of my paper are to describe the larva of *Cononotus* and to reevaluate the systematic relationships of the Cononotidae.

Cononotus bryanti Van Dyke
(Figs. 1-12)

Later instar larva. Body elongate, weakly moniliform, about 1.5 times wider than thick, broadest from abdominal segments 3 to 8; cuticle weakly sclerotized, white; cranium and legs lightly sclerotized, pale creamy; peristomal margin, mandibles, urogomphi and associated tergal pits sclerotized, pale tan.

Cranium about 1.8 times broader than long with broadly rounded anterior corners, dorsoventrally flattened, about twice as broad as thick, without ocelli (Figs. 1-2); glabrous except for few dorsal pairs of setae near base of labrum, and antennal insertions, and several setae laterally and ventrally near antennal insertions and mouthparts; epicranial suture lyre-shaped, demarked by narrow unpigmented zone except anteriorly; epicranial stem short, arms terminating before epistomal margin behind antennal insertions; frontoclypeal suture absent, clypeal margin slightly emarginate; gula narrowed anteriorly, continuous with submentum (Fig. 2). Antennae (Figs. 1, 3) articulated by broad membrane with slight prominences at lateral corners of cranium; 1st segment broader than long, 2nd segment slightly longer than broad,



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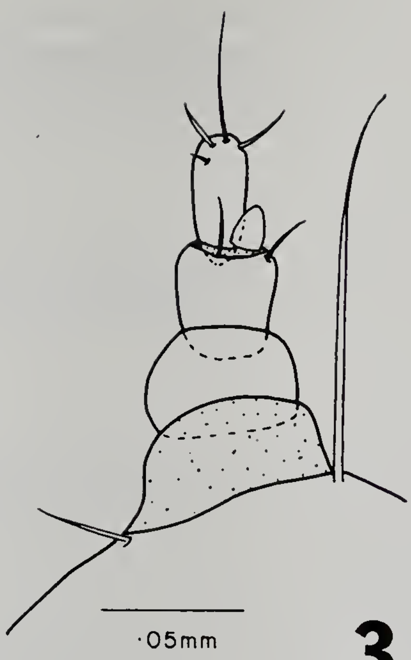

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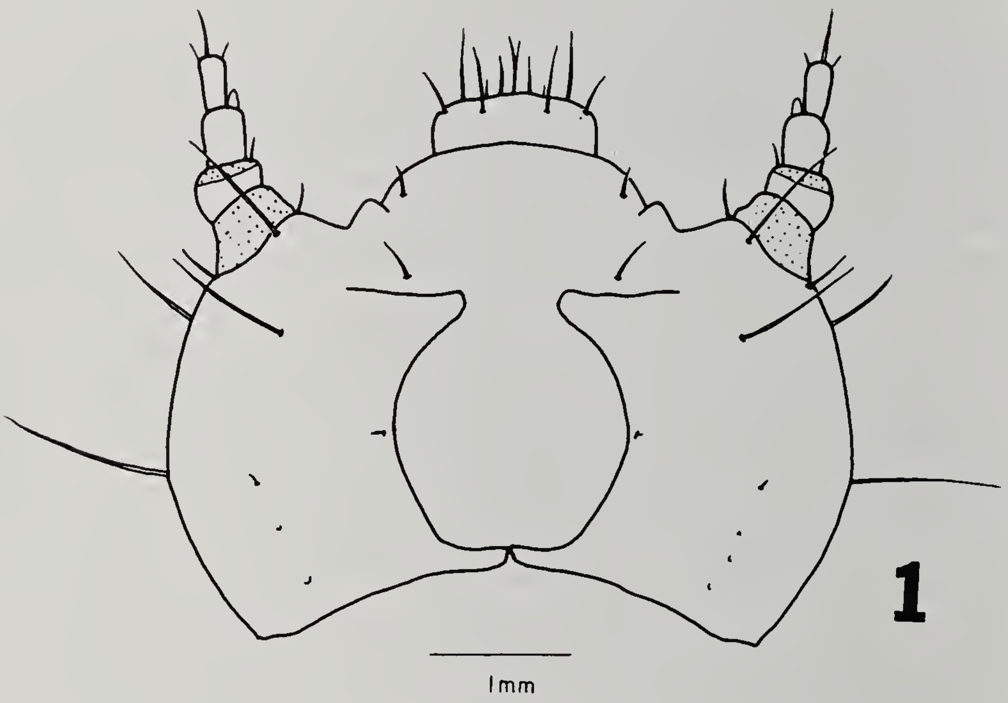

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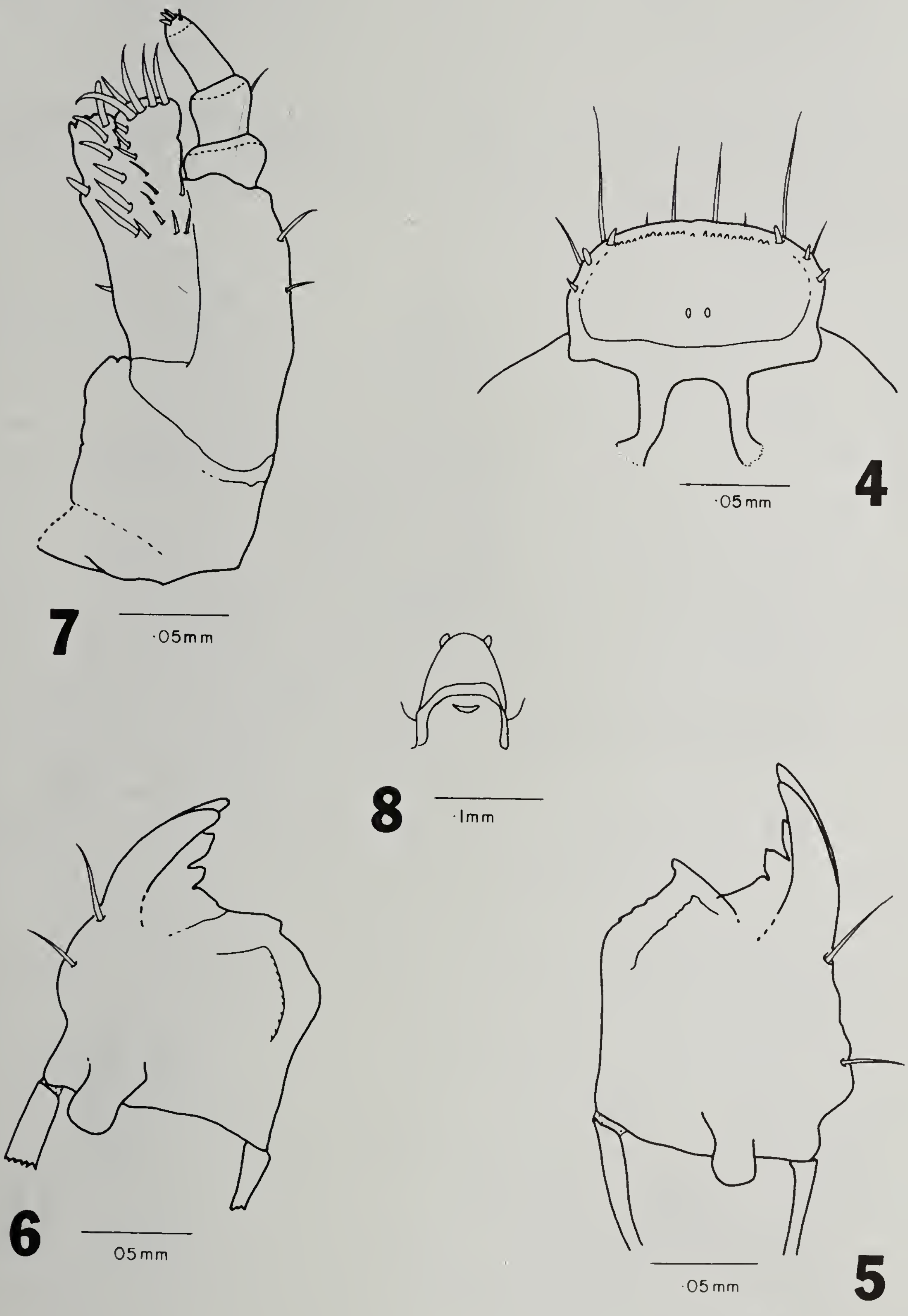
Figs. 1-3. Cranial structures of *Cononotus bryanti*: Fig. 1, dorsal aspect of cranium; Fig. 2, ventral aspect of cranium and mouthparts (semidiagrammatic); Fig. 3, ventral aspect of right antenna.

with acutely rounded peg and pair of short setae situated ventrolaterally on apex; 3rd segment about 2.6 times longer than broad, terminated by one long and several short setae. Labrum (Fig. 1) lightly sclerotized, nearly glabrous except for sparse marginal row of long setae; epipharynx (Fig. 4) with weakly sclerotized posterior baculus continuous with tormae, anterior margin bordered laterally by three pairs of short blunt setae and medially by row of minute denticles, central area with 2 sensillae. Mandibles (Figs. 5, 6) slightly asymmetrical, the left with more prominent anterior molar ridge; incisor lobe with 2 sharp apical teeth and 2 distinct subapical ones. Maxillae (Figs. 2, 7) stout, fleshy, protruding slightly below cranium; cardo indistinctly divided into subtriangular lobe apically, narrow, strut-like lobe basally; mala apically incised, lightly sclerotized apically and bearing 2 subparallel rows of setae; lateral lobe with tuft of 4-6 larger setae on apex, medial lobe with irregular sclerotized margin, but without clearly defined uncus; maxillary palp with apical segment almost as long as basal segments combined, bearing cluster of sensory cones apically. Labium with mentum and submentum membranous, undivided (Fig. 2); ligula bluntly rounded, projecting anterad of labial palps; hypopharyngeal sclerome (Fig. 8) narrow, transverse, without distinct teeth or associated setae.

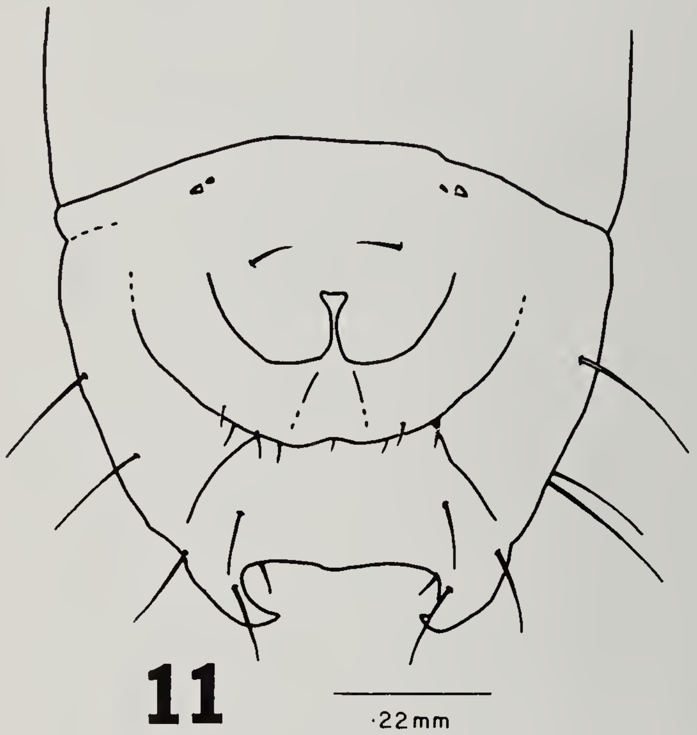


Figs. 4-8. Mouthparts of *Cononotus bryanti*: Fig. 4, ventral aspect of labrum showing epipharynx; Figs. 5-6, ventral aspect of left and right mandibles, respectively; Fig. 7, dorsal aspect of right maxilla; Fig. 8, dorsal aspect of hypopharynx.

Thorax slightly narrower than abdomen; prothorax about 1.3 times as wide as long; mesothorax and metathorax each about twice as wide as long; length ratios of segments: 1.6 : 1.0 : 0.9. Terga and sterna indistinct; coxae very short, oval, separated by about 2.5 diameters. Legs (Fig. 9) short, weak, without exceptional setation or other armature.

Abdomen with anterior 2 segments slightly narrower than succeeding ones; segments 3-8 subparallel, slightly moniliform; segment 9 abruptly narrowed to urogomphi; segments 1-8 glabrous except for pair of setae posterolaterally on each side; segment 9 bearing sclerotized urogomphi recurved dorsally and medially (Figs. 10, 11); urogomphi separated basally by paired, sclerotized, excavated plates, invaginated anteriorly beneath cuticle; 1 pair of setae situated dorsally before urogomphi, several pairs laterally and 2 pairs on bases of urogomphi; sternite 9 U-shaped, bearing 2 pairs of teeth laterally near the base, one member of each pair larger; segment 10 small, enclosed by segment 9 (Fig. 11), indistinctly bilobed. Spiracles (Fig. 12) annular biforous with a single row of air tubes around atrium.

Body length, 4.8 mm.



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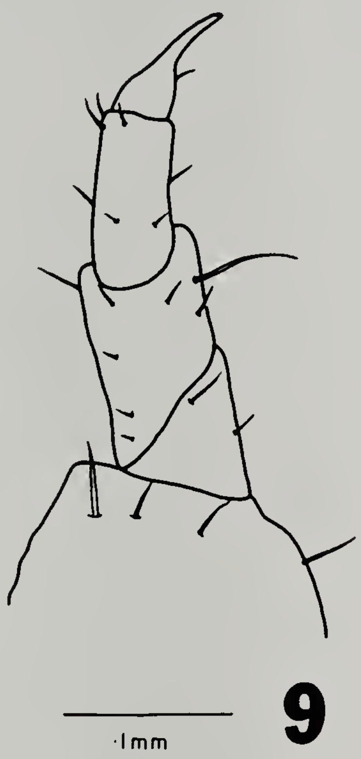

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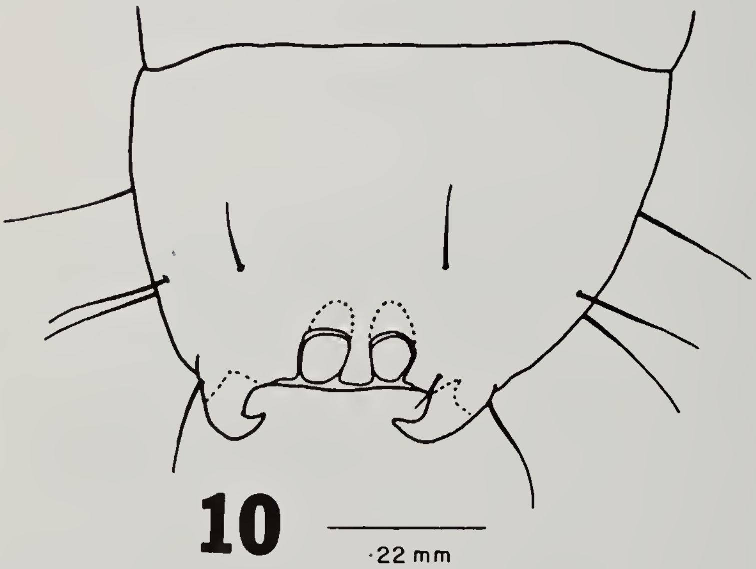

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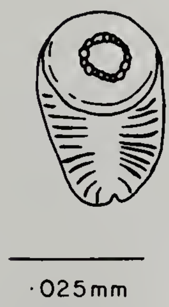

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Figs. 9-12. Thoracic and abdominal structures of *Cononotus bryanti*: Fig. 9, right foreleg; Figs. 10-11, abdominal apex, dorsal and ventral aspects, respectively; Fig. 12, abdominal spiracle.

Material examined. 2 larvae reared from adults collected in Mexico, Baja California, Miller's Landing. April 6, 1976. J. Doyen. The adult beetles were abundant beneath dried cow dung on the coastal sand dunes at Miller's Landing. In the laboratory they were confined in plastic containers of sand which was dampened through a subsurface reservoir of plaster. The larvae, which were preserved August 24, 1976 were in the zone of moist sand adjacent to the reservoir. In nature the larvae, which show no adaptations for living in sand, presumably occur in decaying succulent vegetation or some similarly protected place.

Discussion

The most distinctive feature of the larva of *Cononotus* is the structure of the abdominal apex. The urogomphi are separated by sclerotized, excavated plates which are partly invaginated anteriorly into the 9th tergite; the 10th sternite bears 2 pairs of short, sclerotized spurs basolaterally (Fig. 11). Very similar tergal plates are present in *Agnathus* (Mamaev 1976) and *Pedilus* (Mamaev 1976; Wharton 1979). Mamaev illustrates similar structures in *Pogonocerus* (Pyrochroidae), and elliptical, sunken patches occur between the urogomphi of *Neopyrochroa* (Böving and Craighead 1931; Young 1975). Basally on the 9th sternite of *Cononotus* are 2 pairs of small, laterally directed, sclerotized teeth. A pair of spurs is described in the same position in *Pedilus inconspicuus* (Horn) by Wharton (1979), but not in *Pedilus* sp. by Mamaev (1976), who mentions a row of denticles on the anterior margin of sternite 10. A pair of prominent subapical spurs are illustrated on sternite 10 in *Pergetus campanulatus* (Böving and Craighead 1931). Denticles margin the anterior border of sternite 10 in *Pytho* and *Neopyrochroa* (Böving and Craighead 1931; Young 1975). Moreover, the topological arrangement of the terminal abdominal segments is generally similar in all the taxa mentioned above, with tergite 9 large, sternite 9 small, U-shaped and partly enclosed by tergite 9 or sternite 8. Segment 10 is reduced and at least partly enclosed by sternite 9. Somewhat similar abdominal configurations occur in Mycteridae, Salpingidae, and Othniidae.

Based on selected characters of larvae, the highest phenetic similarities of *Cononotus* are with *Pedilus* and Pyrochroidae (Table 1). All possess a large conical appendage on antennal segment 2 and share a highly similar body configuration and mouthpart structure. In *Cononotus* and *Pedilus inconspicuus,* the maxillary mala is apically cleft, with the inner margin slightly corneus and irregular dentate (Fig. 7) but without a defined uncus.

The apparently low similarity of *Agnathus* to *Cononotus* and *Pedilus* is probably partly due to lack of detailed knowledge of some of its larval structures. The striking similarity in urogomphi and intraurogomphal plates suggests that *Agnathus* is related to *Pedilus*, rather than to the anthicid group. Some characters such as the condition of the maxillary mala (cleft or not) should be re-examined in *Agnathus*. *Pergetus* clearly is more similar to Anthicidae than to the *Pedilus* group, but it shares several features with Pyrochroidae as well. Thus, for the characters compared here, Pyrochroidae shows high similarities to both the *Pedilus-Cononotus* group and to the anthicid group. However, its highest average similarity is to the *Pedilus-Cononotus* group.

On the basis of adult structures, Crowson (1969) suggested that Cononotidae were probably close to Mycteridae. Larval similarities between those taxa include a high level of congruence in the mouthparts, including

Table 1.

Characters	1		2			3			4		5			6			7		
Taxa	a	b	a	b	c	a	b	c	a	b	a	b	c	a	b	c	a	b	c
Anthicidae	x		x			x			x		x					x			x
Pedilidae (Pergetus)	x				x	x			x		x					x		x	
Pyrochroidae	x				x		?		x		x			x	x		x		
Mycteridae		x	x		x			x		x	x		x		x	x			x
Salpingidae	x		x				?			x		x				x			x
Agnathus	x		x				x		x			?		x				?	
Cononotus		x		x				x	x			x		x			x		
Pedilidae (Pedilus)	x	x		x			x		x			x		x			x	x	

Table 1. Selected characteristics of larvae of *Cononotus* and related groups of Coleoptera. Numbered characters and character states as follows: 1. Maxillary mala: a, entire; b, cleft. 2. Maxillary mala: a, membranous; b, irregularly serrate; c, inner margin with uncus. 3. Hypopharyngeal sclerome: a, trapezoidal or subquadrate, cup-shaped; b, rectangular with tufts or ring of setae; c, transverse, band-shaped. 4. Antennal appendage: a, large, conical; b, small, dome-shaped or absent. 5. Spiracles: a, annular; b, annular-biforus; c, annular with peripheral air tubes. 6. Intraurogomphal pits: a, present, well defined; b, ill-defined; c, absent. 7. 9th sternite armature: a, transverse row of denticles; b, 1-2 pairs basal spurs; c. other.

Taxa scored for more than a single character state are variable for that characteristic. Question marks indicate lack of observations, or vague, inconclusive descriptions. Data for all taxa except *Cononotus* were extracted from literature.

the apically cleft mala. However, in mycterids the antennal appendage is very short and dome-like, the spiracles are annular with or without associated air tubes, and the urogomphi and other terminal abdominal structures are not very similar to those of Cononotidae.

Abdullah (1974) synonymized Cononotidae under Anthicidae, without clearly specifying his reasons. Among the characters considered here, *Cononotus* and *Agnathus* share only the presence of a large antennal appendage with Anthicidae. Other observed similarities are common to the entire anthicid-mycterid group of families, and are probably plesiomorphic. Furthermore, Cononotidae and Anthicidae are strikingly different in structure of the terminal abdominal segments, and they differ in the structure of the spiracles, the hypopharynx, and the maxilla.

The pattern of similarities in larval characters suggests that *Cononotus* and *Agnathus* should be included in the Pedilidae, as concluded by Mamaev (1976). Indeed, the larva of *Cononotus* is scarcely distinguishable from that of *Pedilus inconspicuus*. Furthermore, the larvae of all three genera are at least as similar to Pyrochroidae and Mycteridae as to Anthicidae *sensu stricto*. Thus, Pedilidae (=Anthicidae, Pedilinae of authors) should be recognized as a separate family, with the two subfamilies Pedilinae and Cononotinae. *Pergetus* shares most characters with Anthicidae, others with the pedilid-pyrochroid group.

Many of the peculiarities of adult *Cononotus* are probably adaptations to flightlessness and aridity. For example, the connation of the anterior abdominal sternites and tight interlocking of the sternites with the elytra may increase water retention ability. External closure of the mesocoxal cavities by the sterna, rather than by the mesepimeron, occurs in various Heteromera, and is sometimes associated with flightlessness. For example, various intermediate degrees of sternal closure occur in the tenebrionid tribe Anepsiini (Doyen and Lawrence 1979). Those species with the cavities closed or nearly closed by the sterna are flightless.

LITERATURE CITED

ABDULLAH, M. 1974. My concept of the beetle family Cononotidae Crowson = Anthicidae (Coleoptera)—a new interpretation of the old observations. Coleopt. Bull., 28:17-25.

ARNETT, R. H., JR. 1968. The Beetles of the United States. Amer. Ent. Inst., Ann Arbor, Mich. xii + 1112 p.

BÖVING, A. G. AND F. C. CRAIGHEAD. 1931. An illustrated synopsis of the principle larval forms of the order Coleoptera. Ent. Amer., 11:1-351.

CROWSON, R. A. 1953. The classification of the families of British Coleoptera. Ent. Mon. Mag., 89:37-59.

CROWSON, R. A. 1967. The Natural Classification of the Families of Coleoptera. Classey Ltd., Middlesex, England. 1969.

CROWSON, R. A., AND M. G. DEVIEDMA. 1969. Observations on the relationships of the genera *Circaeus* Yablok and *Mycterus* Clairv. with a description of the presumed larva of *Mycterus*. EOS, 40:99-107.

DOYEN, J. T. AND J. F. LAWRENCE. 1979. Systematics and classification of some Tenebrionidae and Zopheridae (Coleoptera). Systematic Entomology, 4: in press.

HATCH, M. H. 1965. Family Pythidae. *In* The Beetles of the Pacific Northwest IV. Univ. Washington Press, Seattle. pp. 84-88.

KITAYAMA, C. Y. 1977. Biosystematics of anthicid larvae (Coleoptera: Anthicidae). M. S. Thesis, University of California, Berkeley.

LECONTE, J. L. AND G. H. HORN. 1883. Classification of the Coleoptera of North America. Smithson. Misc. Coll., 507:xxxviii + 1-567.

KASZAB, Z. 1969. In Freude, H., K. W. Harde and G. A. Lohse (eds.). Die Käfer Mitteleuropas, Bd. 8. Goecke and Evers, Krefeld. 388 p.

MAMAEV, B. M. 1976. Larval morphology of the genus *Agnathus* Germ. (Coleoptera, Pedilidae) and the position of the genus in the system of the Coleoptera. Ent. Rev., 55(3):97-99 (see Ent. Oboz., 55:642-645).

WHARTON, R. A. 1979. Description and habits of larval *Pedilus inconspicuus* (Horn) (Coleoptera: Pedilidae). Coleopt. Bull., 33:27-31.

YOUNG, D. K. 1975. A revision of the family Pyrochroidae (Coleoptera: Heteromera) for North America based on the larvae, pupae and adults. Contrib. Amer. Ent. Inst., 11:1-39.